

A CASE OF MYOPHILY INVOLVING DROSOPHILIDAE (DIPTERA)

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ABSTRACT

The relationship between the xerophytic stapeliad *Caralluma schweinfurthii* (Stapelieae, Asclepiadaceae) and certain species of Drosophilidae (Diptera) has been studied under semi-natural conditions. Data on the plant, the insect visitors and the adaptation involved in terms of pollination ecology are given. Seven species of *Drosophila* and two species of *Zaprionus* are deceptively attracted to the flowers which chemically mimic the natural breeding substrate. This appears to be the first reported instance of myophily involving Drosophilidae. Evolutionary aspects are briefly discussed and the need for field observations emphasized.

UITTREKSEL

'N GEVAL VAN MIOFILIE WAT DROSOPHILIDAE (DIPTERA) RAAK

'n Studie, onder semi-natuurlike toestande, is gemaak van die verhouding tussen die xerofitiese plant *Caralluma schweinfurthii* (Stapelieae, Asclepiadaceae) en sekere spesies van die Drosophilidae (Diptera). Gegewens oor die plant, die insekbesoekers en die aanpassing ten opsigte van bestuivingsekologie word aangebied. Sewe spesies van *Drosophila* en twee van *Zaprionus* word op 'n misleidende wyse tot die blomme aangelok deur na-apery van die voedingsmedium. Hierdie blyk die eerste aangemelde geval van miofilie te wees wat Drosophilidae impliseer. Ewolutionele aspekte word kortliks bespreek en die behoefte aan verdere veldstudies beklemtoon.

INTRODUCTION

Stapeliads (tribe Stapelieae, family Asclepiadaceae) are a characteristic feature of the African flora, with many hundreds of species in over a score of genera known (White and Sloane, 1937). A few species are known from adjacent areas, but the majority are concentrated in Africa with the arid parts of southern Africa being very rich in species: sixteen of the twenty genera described by White and Sloane have representatives there. There is extensive variation between flowers of the various species as regards colour, patterning, size, type and distribution of hairs, surface sculpture of corolla and other features. This strongly suggests adaptation to specific pollinators as Proctor and Yeo (1973: 300 *et seq.*) have pointed out. Little is known, however, concerning the pollination ecology of stapeliads, apart from the observation that some of the larger species, for example *Stapelia gigantea* N. E. Brown and *Stapelia nobilis* N. E. Brown, attract carrion flies by means of their deceptive floral odour. The deception in this case is so effective that oviposition around the central disk of the flower

often occurs. As the stapeliads have pollinaria (i.e. pollinia with associated structures) rather like those of Orchidaceae, there is thus an interesting opportunity for research into the determination of their pollinators and the relationships between the two.

In the case described here, a hitherto unreported group of pollinators, namely Drosophilid flies, is shown to be active in pollination and thus the spectrum of stapeliad myophily (adaptation to pollination by flies) is broadened. The attraction based on odours simulating decomposing organic matter, or the natural breeding substrate, has led to the further distinction of sapromyophily, so that this term could just as well be applicable in the present case.

MATERIAL AND METHODS

1. *The myophilous plant*

The case described involves the small, leafless xerophyte *Caralluma schweinfurthii* Berger. It has recently been shown (Leach and Plowes, 1966) that this species includes *Caralluma piaranthoides* Obermeijer.

The plant is a small, jointed, procumbent perennial consisting of soft, fleshy stems growing up to 5 or 6 cm above the soil in which it is shallowly rooted. The species is widely distributed in central and south-central Africa. The known distribution, taxonomic citations and details of flower structure are given by Leach and Plowes (1966) while a colour photograph of the flower has been published by Plowes (1971:10). Observations were made on a cultivated plant of unknown origin, grown outdoors in Johannesburg during the period 19 February to 4 April, 1973 when the plant was in flower. The months of February and March are the regular flowering period of the plant in Johannesburg and these months, when the weather is warm and humid, correspond with the peak time of drosophilid activity in the area.

The plant was observed intermittently over the period mentioned previously for a total of ca 6 hours during daylight.

2. *The insect visitors*

Visitors were aspirated individually from the flowers and preserved in alcohol for cataloguing and later identification. For a few days, while the plant was kept indoors, a trap of rotting pineapple (*Ananas comosus* L.) seeded with yeast suspension was set up outdoors to sample the local insect population attracted to such bait. Specimens were netted, preserved, catalogued and identified as before. A few drosophilids bearing pollinia were prepared for scanning electron microscopy by dehydration and subsequent coating with gold; these were viewed and photographed in a Cambridge 'Steroscan' instrument.



FIG. 1.
Flower of *C. schweinfurthii*.
Scale = 5 mm

RESULTS

1. *Visitors*

Drosophilids were avidly attracted to the flowers for a few hours after sunrise and before sunset. At these cooler times of the day the flies were very active on the flowers which emitted a strong odour variously described as "over-ripe fruit with hint of orange" and "sour beer". It may be noted that it is well-known that a particular flower can evoke seemingly different olfactory responses in different persons, as judged by their responses. During the heat of the day, flies were not active and odour could not be detected. No insects other than *Drosophilidae* were observed to be attracted to the flowers. There was no differential attraction between the sexes of the visitors, and both males and

females appeared to be equally capable of acting as carriers of pollinia. Even while the plant was kept indoors for a few days, a few flies still managed to find their way to the plant, showing that even over some distance the flowers effectively advertise their presence.

A careful search for deposited eggs was made on the flowers and none was found, so it may be concluded that oviposition does not take place on the flowers; possibly, the appropriate tactile responses needed for this are absent. It may be noted that oviposition always occurs on fruit-traps.

The results of sampling drosophilids visiting both flowers and fruit-trap are given in Table 1.

TABLE 1.

DATA ON VISITORS: NUMBERS OF DROSOPHILIDAE, BY SPECIES, CAUGHT ON FLOWERS OF *CARALLUM SCHWEINFURTHII* AND TRAPPED WITH FRUIT BAIT

	with (+) pollinia	flowers	traps	total	χ^{2**}
<i>Drosophila busckii</i> Coquillett	—	0	6	6	7,85
<i>Drosophila immigrans</i> Sturtevant	+	62	40	102	0,74
<i>Drosophila melanogaster</i> Meigen (males)	+	2	2	4	0,37
<i>Drosophila</i> sp. (repleta group)*	—	2	1	3	
<i>Drosophila punctatonevosa</i> Frey	—	2	0	2	
<i>Drosophila simulans</i> Sturtevant (males)	+	21	10	31	1,57
<i>Drosophila melanogaster</i> + <i>simulans</i> (females)	+	13	10	23	0,00
<i>Zaprionus tuberculatus</i> Malloch	—	6	10	16	2,37
<i>Zaprionus vittiger</i> Coquillett	+	8	10	18	1,08
		116	89	205	13,98***

* Possibly an undescribed species—specimens catalogued under WWR 20G.

** χ^2 computed by apportioning the total catch for each species, weighted according to the column totals to give expected numbers in each cell, on the assumption of no differential attractivity.

*** d.f. = 6; 0,05 > P > 0,01.

The results of trapping on the flowers and in the fruit-trap were compared by means of a χ^2 -test of homogeneity. The test shows a significant difference between flowers and trap regarding the capabilities for attracting the different species. However, it is clear that one species, *D. busckii*, contributes more than half the total χ^2 -value and this species is known to breed in proteinaceous substrates. The presence of *D. busckii* at the fruit-trap is doubtless due to opportunistic feeding, while the other species represent true fruit-breeding species and behave in accordance with the hypothesis that the flowers are as

attractive to them as the fruit. The χ^2 -values for the remaining species are each non-significant. It may be concluded that the flowers, by simulating the odour(s) of the natural breeding substrate, mimic the latter and effectively deceive the drosophilids into visiting the plant when in flower.



FIG. 2.

Drosophila punctatonervosa visiting flower; note unopened bud.
Scale = 5 mm

2. Results on pollination

The flower (Fig. 1) is small, in colours of yellow and maroon. Excepting a few older stems, each one of about 40 stems carried a few clusters of buds (2–6 buds per cluster) in various stages of development although only a few flowers were open simultaneously. According to Leppik's (1968) morphogenetic classification, the flower belongs to his class 4: pleomorphic, showing radial symmetry and at the pluriform evolutionary level, but a specialised form deviating from the general trend.

In the bud stage, the five corolla lobes are connate at the tips, as may be seen in Fig. 2. As soon as the first lobe started peeling back, flies would enter the chamber formed by the remaining lobes, so that by the time the flower was fully

opened all the pollinia had been removed. One flower, specifically watched, had all five pairs of pollinia present at 0600 and all removed at 0645 hours. Removal of pollinia is thus rapid. Attachment of the pollinaria (pollinia plus associated structures) to the proboscis of the fly takes place while the fly is tapping with the proboscis on the corona (Fig. 2). Eight individuals, belonging to several species (Table 1) were recovered with attached pollinia; in one case (Fig. 3), two pairs of pollinia were attached to a single fly. None of the captured specimens with pollinia had them attached anywhere but on the proboscis, where the corpusculum and retinacula (or translator arms) were affixed to the shaft of the proboscis. The attachment appears to be a firm one as individuals with pollinia, kept alive overnight in glass vials, did not lose them. Little inconvenience appeared to be caused to the insect, and behaviour appeared normal, as suggested by the observation that one fly (*Zaprionus vittiger*) had managed to pick up two pairs. On one occasion, a fly with pollinia on a front leg was observed on a stem of the plant: the front legs were being rubbed together as if in an effort to dislodge the attached masses. How they got there in the first place is not known.

Actual pollination, that is release of the pollinia onto a recipient flower, was unfortunately not observed. It is possible, even likely, that there must be a time delay between picking up the pollinia and their release in order to minimize the likelihood of self-pollination. This delay could operate by means of a mechanism involving maturation of part of the associated structures which attach the pollinia to the vector. It is not known whether the plant is self-sterile or not as no artificial pollinations were done. At any rate, even under the best of conditions, the rate of effective delivery of pollinia must be very low, as in the case with orchids where the mechanism is similar. As the pollen is delivered *en masse*, van der Pijl and Dodson (1966) have described this as a "dangerous gambling-mechanism of a long-term strategist". However, in this precision gambling there is ultimate efficiency because if the pollinia are actually delivered, only one visit is required to fertilize hundreds or thousands of ovules.

In the present case, release of pollinia would most likely take place near the corona which is the appropriate place for growth of the pollen tubes to effect fertilization; here the structure of the corona is such that the pollinia would be engaged by the anther wings for detachment. As collecting disturbed the whole aggregation of flies each time, many of the carriers probably did not return to the flowers. Certainly only a small fraction of the very many pollinia removed were recovered by capture of flies bearing them.

DISCUSSION

Two important points arising from the preceding sections and the evolutionary significance of the adaptation require discussion.

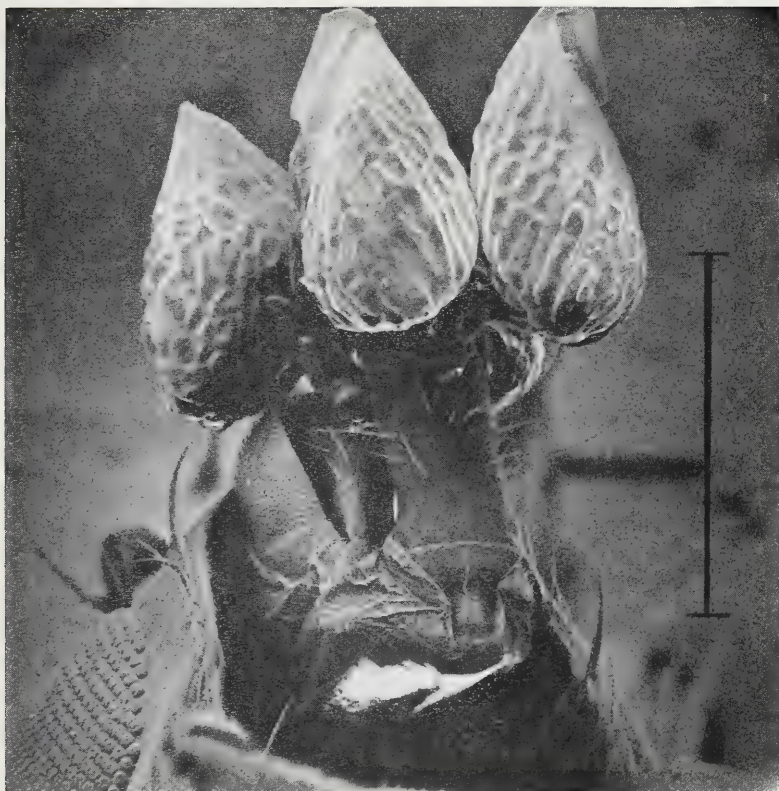


FIG. 3.

Ventral view of head of *Zaprionus vittiger* showing two pairs of attached pollinia.
Scale = 0,5 mm

1. *Is the case a genuine one of myophily?*

According to Faegri and van der Pijl (1966), myophilous flowers are adapted for pollination by flies, and exhibit a complex of characteristics associated with this adaptation; the complex describes a syndrome. Twelve features which may contribute to a complex have been given by these authors (op. cit.), although not all may be present in any specific case. The syndrome of myophily is well-developed in certain genera of the Asclepiadaceae and Orchidaceae (Faegri and van der Pijl, 1966; van der Pijl and Dodson, 1966); in the latter family, four

large groups in the most divergent genera have become myophilous, indicating that the adaptation has repeatedly arisen independently.

In the case described here, features positive (+) for these are tabulated below:

General syndrome of myophily (from Faegri & van der Pijl, 1966)	Present case (<i>C. schweinfurthii</i> flowers)
A. Anthesis at different times	+
B. No zygomorphy; radial flat or trap-like	+
C. Large landing surface with osmophores	+
D. Colour dull or greenish, occasionally augmented by brown-purple with checkered or dotted designs	+
E. Odour putrescent	+
F. Nectar or other food usually absent	+
G. No nectar guides	+(*)
H. Perianth often with slits or holes in side	—
I. Perianth often with transparent window-guides	—
J. Brown furry hair cover	—
K. Vibratile hairs ("Flimmerkörper" or oscillators)	—
L. Trap devices guiding visitors or catching or holding them	+

* A flower preserved in alcohol was viewed under UV light (wavelength 254 nm) and no guides were visible.

Characters H–L inclusive tend to be shown in flowers that physically trap the visitors, which does not happen in this case. Thus the evidence from: (a) chemical mimicry of the feeding (and for the drosophilids sampled, also breeding) substrate; (b) positive attraction of potential pollinators; (c) capture of five different species carrying pollinia; (d) features of the flower indicative of myophily; and (e) correspondence between flowering time and peak drosophilid activity allows of the conclusion that *C. schweinfurthii* is, indeed, specifically adapted for pollination by Drosophilidae.

2. Which species of Drosophilidae are the actual pollinators in the field?

The observations reported here do not necessarily establish that any or all of the visitors are the actual pollinator(s) where the plant grows naturally. The objection that the plant was studied out of its natural area of occurrence loses most of its validity when it is borne in mind that the species listed in Table 1 (with the possible exception of *D. punctatonervosa*) are widespread over all of central and southern Africa. Two points must be borne in mind here: firstly, experience with other entomophilous flowers indicates that it is unlikely that the plant is monophilic or strictly tied to a single pollinator, although such cases do occur. Rather, it would appear that it may well be oligophilic or adapted

to a group of similar (in size) or closely related species which, as an evolutionary strategy, would be safer for long-term survival. The fact that several drosophilid species of more or less similar size can pick up the pollinia would support this view. Secondly, some of the species listed in Table 1, for example *D. immigrans*, *melanogaster* and *simulans*, are colonizing species and are now virtually cosmopolitan; their geographic origin is uncertain (Dobzhansky, 1965). The *Zaprionus* species, however, are restricted to Africa (ten or more species) and south-east Asia (a few species) and may well be effective pollinators in the wild. The species *Z. tuberculatus* and *Z. vittiger* are widespread in Africa. Information as to the actual pollinator(s) can come only from field studies, but it is clear that whatever species are actually involved the plant is adapted to small, fruit-breeding drosophilids.

3. Evolutionary aspects

Van der Pijl and Dodson (1966) have drawn attention to the fact that sapromyophilous flowers are most numerous in warm arid zones especially in Africa but that, curiously, this switch to Diptera is not paralleled in similar zones in the Americas; they suggest that the switch to Diptera in Africa is a long-standing one related to the dominance of flies there. It would thus be of great interest to have comparative information on the pollination ecology of the numerous stapeliads occurring in Africa as this would, doubtless, show an evolutionary connection between their radiation and that of Diptera.

It is very likely that there are no fewer than 2 000 extant species of *Drosophilidae* (Hardy, 1965; Wheeler and Hamilton, 1972) with about half of the known species in the large genus *Drosophila* Fallén; these have been the subject of a large number of investigations conducted in both the laboratory and field. As is to be expected, there is a wide diversity of ecological niches exploited for both feeding by the adults and for nutritional support of the larvae during development. Breeding sites are typically fallen fruit, fleshy fungi, flowers (both fresh and fallen) or other plant material in the initial stages of decay where associated yeasts and bacteria are consumed by the drosophilids. While feeding by adults is opportunistic the breeding sites tend to be more carefully selected with the behaviour of the ovipositing females accordingly adapted and some species are exceedingly specialised in this regard. To date, the reverse situation, namely where a particular plant species is specifically adapted for pollination by drosophilids has not been described. Such a case, described here, is therefore of double interest, both to students of evolution in stapeliads and drosophilids.

It is known (Free, 1970) that drosophilids may be effective in the pollination of certain field crops, for example guayale (the composite *Parthenium argentatum*

A. Gray), and some of the flower-breeding drosophilid species may be incidentally involved in pollination, but none of these cases shows specific adaptation entirely on the part of the flower, which is the essential feature of myophily.

Of particular interest in the present case is the observation that while Drosophilidae are deceived into investigating the flowers, wastage of eggs does not occur (as it does with the larger carrion flies) and thus the deception is not counterselective to responsive insects. This suggests that the adaptation is a long-standing one, more ancient than the one between the larger stapeliads and carrion-flies.

CONCLUSIONS

1. The flowers of *Caralluma schweinfurthii* are adapted for pollination by drosophilids ("fruit-flies").
2. The insect visitors are attracted by chemical mimicry of the natural breeding and/or feeding substrate, i.e. the relationship is one of sapromyophily.
3. Nine species of Drosophilidae in two genera were observed to visit the flowers, and four of the species were observed to act as pollen-vectors.
4. The need for field observations over the range of the plant's distribution is emphasized in order to confirm or modify the above findings.
5. The case described is the first reported one of myophily where Drosophilidae are involved.

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